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Effects of UV-B radiation on germination characteristics in invasive plants in New Zealand

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Abstract

UV-B radiation represents a potentially selective, yet little studied environmental factor for plant invasions, especially with respect to germination characteristics and seedling establishment in areas of high UV-B exposure such as New Zealand. To explain invasive potential of plant species pre-adaptation and local adaptation to selection factors in the invaded range are two frequently consulted concepts. To test for the relevance of these mechanisms, it is necessary to compare both invasive and non-invasive species, as well as native and exotic origins of invasive species. In the present study, germination success of two congeneric species pairs of the genera *Verbascum* (Scrophulariaceae) and *Echium* (Boraginaceae) were investigated under high UV-B intensities. Each genus comprised one species that has successfully invaded New Zealand grasslands and one species that was introduced but has not been invasive in New Zealand. In an among-species approach, pre-adaptation was tested by comparing germination success of native (European) origins of all four species in relation to their different invasive success in New Zealand. In a within-species comparison, native (European) and exotic (New Zealand) origins of the two invasive species were compared to test for local adaptation to UV-B in the invaded range. In both approaches, UV-B radiation inhibited the germination success of all study species. However, the comparison of invasive and non-invasive species of the two genera showed no UV-B-specific pre-adaptation of invasive species to high

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UV-B intensities. Higher germination success of invasive species probably led to an establishment advantage during colonization of the invaded range. Although local adaptation of exotic populations to UV-B could not be demonstrated in the within-species approach, a genetic shift in germination velocity between native and exotic origins was found. These differences may be ascribed to other relevant environmental factors, e.g. overall irradiation and drought, inducing similar plant responses as under UV-B radiation.

Keywords

Congeneric species pairs, *Echium*, invasive vs. non-invasive species, local adaptation, native vs. exotic origins, pre-adaptation, *Verbascum*

Introduction

In the course of globalization, a plethora of species have managed to overcome geographic barriers and to successfully establish wild populations in the new environment. Most notably, this can be observed in previously isolated systems, such as Australia, New Zealand, Madagascar and other islands (Loope and Mueller-Dombois 1989). Following the framework for biological invasions proposed by Blackburn et al. (2011), the environmental conditions in the invaded range represent an important barrier a species has to overcome upon arrival in a new region before it can become invasive. One of the most prominent research goals in invasion ecology is to identify which plant species have the potential to respond successfully to novel environmental conditions in new habitats and which mechanisms are underlying the success or failure of invasions. Two mechanisms that might apply non-exclusively have been repeatedly addressed, i.e. the concept of pre-adaptation including species sorting following environmental filtering (Theoharides and Dukes 2007, Shine et al. 2011) and the role of adaptive evolution following natural selection (Prentis et al. 2008, Buswell et al. 2011). In fact, some species are pre-adapted to become invasive as they have evolved traits in their native regions that confer an advantage in the introduced range (Fridley 2013). In contrast, some species evolve new traits in response to new environments (Erfmeier et al. 2011). Evidence for pre-adaptation can be derived from comparing pairs of invasive and non-invasive species within a genus (Schlaepfer et al. 2010, van Kleunen et al. 2011), whereas more recent local adaptation needs to be tested in within-species comparisons of native and exotic origins (Kawecki and Ebert 2004).

In the last decades, many studies have attempted to identify characteristics that explain species' invasiveness. Frequently evoked characteristics are a large native range and the ability of fast dispersal, as induced by short generation times, high seed production, low seed weight and long seed persistence (Rejmánek and Richardson 1996, Dukes and Mooney 1999). Especially reproduction-related traits seem to be closely connected to the establishment success of invasive species. Species equipped with such a set of characteristics are considered predisposed with respect to successful colonization of new environments. Testing for effects of pre-adaptation in plant invasions relies on comparing congeneric species with different invasive potential. For example, a comparative study including 14 congeneric pairs of species native to Europe and inva-

sive in the US revealed faster germination, higher productivity and a higher proportion of flowering plants of the invasive species than of their native congeners (Schlaepfer et al. 2010). Furthermore, invasive *Impatiens* species displayed a shorter stratification period than their native congeners (Perglová et al. 2009). In particular, higher germination rates of invasive species compared to non-invasive congeners have been identified in numerous studies (Cervera and Parra-Tabla 2009, Perglová et al. 2009).

However, germination patterns have also been shown to differ between exotic and native populations, thereby providing evidence for the alternative explanation of local adaptation taking place in the invaded range. There are some examples of herbaceous and woody plants that indicate lower germination rates of native populations compared to exotic ones (e.g. Kudoh et al. 2007, Beckmann et al. 2011, Hirsch et al. 2012), whereas other studies reported differences in germination velocity (Erfmeier and Bruelheide 2005). Hierro et al. (2009), for example, were able to link different germination patterns of native and exotic populations to regional climatic conditions. Such findings could represent non-random introductions of faster-germinating populations. However, such evidences might also indicate genetic differentiation in germination characteristics between native and exotic populations that resulted from selection processes during introduction (Bossdorf et al. 2005).

Invasive species have to face several biotic and abiotic selection factors in the invaded range, such as competition, herbivory, soil properties and climatic conditions (Erfmeier 2013). Nevertheless, the impact of growth-limiting high UV-B levels on invasion processes has rarely been evaluated to date, although UV-B radiation is distinctively higher in the highly-invaded regions of the southern hemisphere such as in Australia or New Zealand (McKenzie et al. 2007) compared to the origin of many invasive plants.

Early stages of plant development and seedling establishment are particularly sensitive to biologically effective UV-B radiation including metabolic limitations or DNA damage, when appropriate protection measures are not yet fully developed. In particular, reduced seedling biomass, inhibited hypocotyl or root development and growth abnormalities (e.g. shoot curvature) have been observed in response to high UV-B intensities (Krizek 1975, Tevini et al. 1983, Tosserams et al. 1997, Dai and Upadhyaya 2002). In addition, species differ in their responsiveness to UV-B radiation. Musil (1995), for example, described higher UV-B resilience for monocotyledons than for dicotyledons. Evidence of UV-B-induced inhibition of germination has been provided by several studies to date (Tevini et al. 1983, Tosserams et al. 1997, Dai and Upadhyaya 2002). There is also clear evidence for inter- and intraspecific differences in UV-B sensitivity in plants (Hofmann and Campbell 2011). However, UV-B sensitivity of invasive species and the consequences for establishment and spread of populations have been studied only rarely. One of the few examples has revealed differential UV-B effects on later stages of growth in a comparison of populations originating from the native and exotic provenances of *Hieracium pilosella* L. (mouse-ear hawkweed, Beckmann et al. 2012). For example, UV-B radiation caused a decreased belowground biomass and an inhibited vegetative reproduction of *H. pilosella* individuals, as well as significant alterations in leaf morphology.

Hence, we conducted a germination experiment comparing pairs of invasive vs. non-invasive species of the genera *Echium* and *Verbascum*, and native vs. exotic origins of the respective successful invader. We tested for pre-adaptation to high UV-B levels in native populations of invasive species as compared to congeneric non-invasive species, and for effects or more recent evolutionary processes, that may hint at local adaptation of exotic populations from New Zealand in the germination responses. We addressed the hypotheses that a) UV-B radiation inhibits germination success in plants and b) that invasive species and exotic populations show higher germination success in comparison to non-invasive species and native populations of invasive species, respectively. In a first analysis, we compared the germination success in response to high UV-B radiation of species native to Europe that are currently invading New Zealand grasslands with non-invasive congeners that, as yet, have failed to spread to a similar degree in New Zealand. In a second analysis, we tested for within-species differentiation among native and exotic origins. Accordingly, we included seeds of native (European) and exotic (New Zealand) populations of *Echium vulgare* L. (blueweed) and *Verbascum thapsus* L. (common mullein), as well as native (European) populations of their non-invasive congeners *Echium plantagineum* L. (Paterson's curse) and *V. nigrum* L. (dark mullein), respectively. This is the first study addressing the role of UV-B for seedling emergence and establishment for plants invasive in the southern hemisphere.

Methods

Study species

We used seeds of two pairs of congeneric species of the genera *Echium* (Boraginaceae) and *Verbascum* (Scrophulariaceae). All four study species are native to Central Europe or distributed in Eurasia and typical components of dry grasslands and ruderal habitats. They are characterized by high drought tolerance and a strong prevalence in open, unshaded habitats (Gross and Werner 1978, Klemow et al. 2002, Sheppard and Smyth 2012). The species of both genera are monocarpic and generally biennial and develop a rosette in the first growing season, whereas a flowering stem sprouts in the second year. In all species, the upper leaf surface is typically piliferous, i.e. *Verbascum* plants are densely covered with woolly, branched stellate trichomes (Gross and Werner 1978), whereas *Echium* leaves are equipped with unicellular, bristly hairs with silicified or calcified cell walls (Möhl 2011). Within each species pair, one species was classified as 'invasive' in the South Island of New Zealand, whereas the other species was considered 'non-invasive' (see Suppl. material 1). For the among-species approach, all European seeds, i.e. native origins, of the invasive and the non-invasive species were investigated. In addition, for the within-species approach, European native origins were compared with New Zealand seeds of exotic origins for *Echium plantagineum* and *Verbascum thapsus*. In total, this resulted in a set of six origins to be tested. Each origin was represented by four populations (except for European seeds of *E. plantagineum*:

n=3 and New Zealand seeds of *E. vulgare*: n=5), i.e. a total of 24 populations. Seeds of the invasive species – *E. vulgare* and *V. thapsus* – were collected in 2011 in grasslands and ruderal habitats between 65–718 m a.s.l., whereas seeds of the non-invasive species – *E. plantagineum* and *V. nigrum* – were obtained from commercial seed companies (for details see Suppl. material 1).

Experimental design and data collection

The germination experiment was conducted at Lincoln University in Lincoln, Christchurch (New Zealand) in March 2012, in a walk-in growth chamber (Type PGV36, Conviron). The UV-B treatment was induced by twelve UV-B tubes (UVB 313 EL, Q-Lab Corporation), which were installed in addition to a standard set of illuminants. Each UV-B tube was enveloped with UV-B-permeable cellulose acetate filter to exclude undesired wavelengths (i.e. UV-C). During the experiment UV-B intensity was measured continuously in the growth chamber by a UV-B sensor, thus, an electronic feedback system kept the intensity constant (Hofmann and Campbell 2012). The irradiance levels were 38.2 kJ m^{-2} d^{-1} biologically effective UV-B, normalised to 300 nm (Caldwell 1971). Half of the seeds were exposed to UV-B by using one frame with six UV-B tubes, while the other half was placed below the second frame where the UV-B tubes were switched off. We installed an UV-B impermeable Mylar® curtain in the middle of the growth chamber to apply UV-B-radiation exclusively to one section of the chamber. Photosynthetically active radiation and UV-B radiation was applied 16 hours a day. During the whole experiment the temperature within the chamber was set at 23 °C with a relative humidity of 95 %.

The germination test was done in seedling trays (i.e. plots) arranged in a split-plot design. Eight seedling trays, filled with sterilized, finely granulated substrate, were each sub-divided in 24 quadrats (5cm × 5cm) being separated aboveground. For origins of *Echium* and *Verbascum*, 12 and 25 seeds per population, respectively, were sown in each quadrat. Each of the 24 populations was sown once per plot, i.e. each population was replicated eight times in total. Half of the plots were exposed to UV-B exposure, whereas the other four plots served as a control, i.e., no UV-B. The plots were randomly positioned within the two UV-B treatments and randomization was repeated twice during the experiment, including reassignment of UV-B applications to the two sections within the chamber.

The seeds were sown on the wet substrate and slightly pressed in. The trays (i.e. plots) were placed in tubs, filled with water, to keep the substrate moist. In addition, the trays were sprayed with water every second day to prevent them from drying out. From the third day of the experiment onwards, the number of germinated seeds was initially recorded daily and later every other day (ten times in total). The last germination event was monitored on day 17. Newly emerged seedlings and cases of seedling mortality were assessed visually. At the end of the experiment, we counted the final number of seedlings in each quadrat and determined the germination success.

Statistical analysis

For data analysis, linear mixed models were applied in SAS 9.2 (SAS Institute Inc. 2000) using the procedure 'mixed' and type 3 sum of squares. Due to a lack of normal distribution, the data for germination success were analyzed following square root transformation (as recommended by Zuur et al. 2009).

Data were analyzed according to an orthogonal design reflecting the hypotheses by first comparing invasive and non-invasive species (among-species approach: n = 15 populations) and secondly, comparing native and exotic origins of the two invasive species *E. vulgare* and *V. thapsus* (within-species approach: n = 17 populations).

For the among-species approach, germination data of native populations of all four investigated species (n = 120 quadrats) were included in the statistical analysis, testing maximum germination success as a response variable. The model included 'genus' (*Echium*, *Verbascum*), 'status' (invasive, non-invasive) and 'treatment' (UV-B, no-UV-B) as fixed factors, whereas 'treatment × plot' and 'genus × status × population' were considered random factors. In order to test for differences in germination velocity, a repeated measures analysis was done by adding 'days' (i.e., the date of seedling census) as a continuous variable and 'genus × status × treatment × unit (location in a certain quadrat)' as a random factor to the model.

For the within-species approach, germination data of native and exotic populations of the invasive species *E. vulgare* and *V. thapsus* were tested for potential differences in UV-B tolerance (n=136 quadrats), applying the same model. Therefore, maximum germination success was tested in a model containing 'species' (*E. vulgare*, *V. thapsus*), 'origin' (DE, NZ) and 'treatment' (UV-B, no-UV-B) as fixed factors. 'Species × origin × population' and 'treatment × plot' were included as random factors. Again, a repeated measures analysis was done for all ten censuses during the experiment, using a similar mixed model but also including 'days' as a continuous variable and 'species × origin × treatment × unit' as a random factor.

All figures were produced with R 3.0.0 (R Core Team 2013).

Results

The among-species approach: invasive vs. non-invasive species

Both genera differed significantly in germination success with a higher maximum germination of the *Verbascum* species ($p < 0.001$, Fig. 1, Table 1). There was a significant effect of status, i.e., in both genera the invasive species – *E. vulgare* and *V. thapsus* – showed a higher final germination than the non-invasive species (p=0.006, Fig. 1a). The non-significant interaction effect of 'genus' and 'status' confirmed the same trend in both genera (Table 1). UV-B radiation caused an overall reduction of germination success in *Echium* and *Verbascum* species (p=0.022, Fig 1b). However, a significant

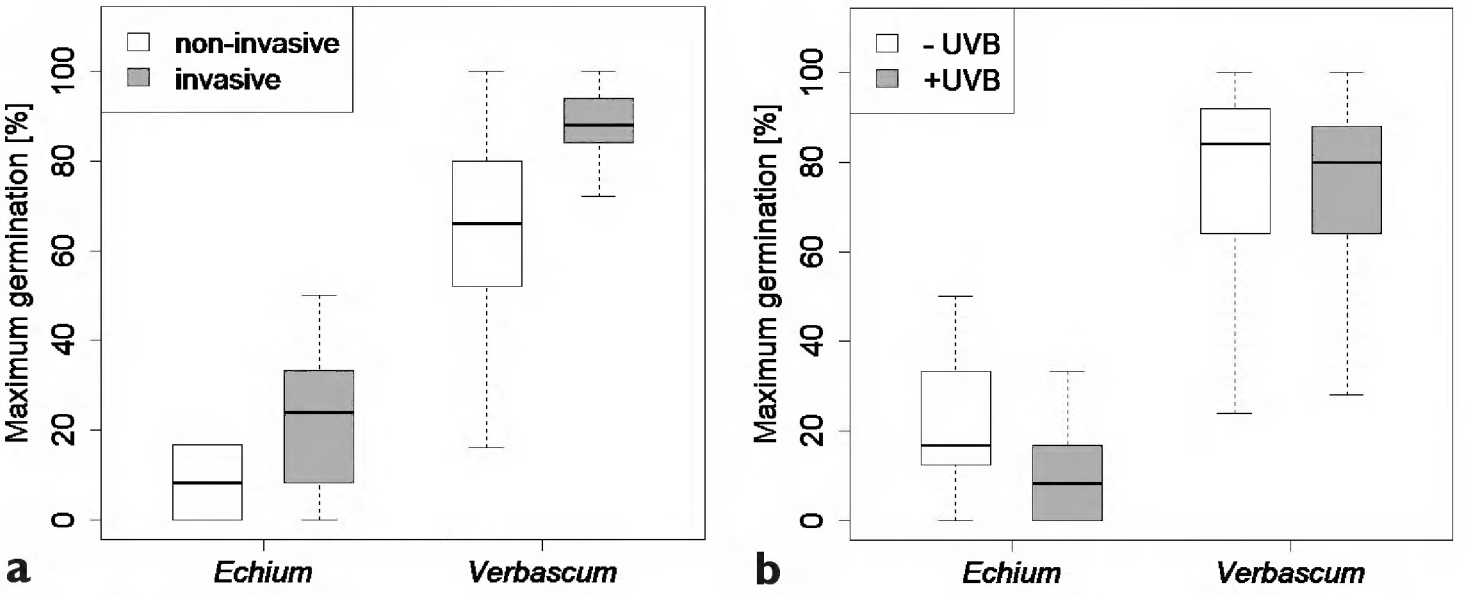

Figure 1. Maximum germination in the among-species approach testing for pre-adaptation of *Echium* and *Verbascum* seeds. **a** of invasive (grey) and non-invasive (white) species and **b** in response to UV-B radiation (grey) and no UV-B radiation (white) treatment.

Table 1. Results of the mixed model analysis of the among-species approach testing for pre-adaptation. Degrees of freedom (df_N = numerator, df_D = denominator), F-statistics (*F*) and significance values (*p*) are given. 'Plot × treatment' and 'genus × status × population' interactions were considered random effects and a Z-value instead of F-value is provided. Bold numbers indicate significant p-values ($p < 0.05$).

Source	df_N	df_D	*F/Z*	*p*
treatment	1	6	9.33	**0.022**
genus	1	11	86.77	**<0.001**
status	1	11	11.35	**0.006**
genus × status	1	11	0.70	0.421
genus × treatment	1	95	11.41	**0.001**
status × treatment	1	95	0.36	0.551
genus × status × treatment	1	95	0.44	0.507
treatment × plot			0.56	0.286
genus × status × population			2.03	**0.021**

'genus × treatment' interaction effect indicated a stronger decrease of germination by UV-B in the genus *Echium* than in the genus *Verbascum* (p=0.001, Fig 1b). There was no evidence for a different UV-B tolerance of both statuses, i.e. between invasive and non-invasive species (Table 1).

Repeated measures analysis confirmed these effects over time (Table 2). In addition, significant two- and threefold interactions among 'days', 'genus' and 'status' suggested a different course of germination of the two statuses in both genera over time (p=0.003, Fig. 2). Thus, *V. thapsus* and *E. vulgare* did not only attain higher germination rates but also germinated more quickly.

Table 2. Results of the repeated measures analysis of the among-species approach testing for pre-adaptation. Degrees of freedom (df_N = numerator, df_D = denominator), F-statistics (*F*) and significance values (*p*) are given. 'Treatment × plot', 'genus × status × population' and 'genus × status × treatment × unit' interactions were considered random effects and a Z-value instead of F-value is provided. Bold numbers indicate significant p-values ($p < 0.05$).

Source	df_N	df_D	*F/Z*	*p*
treatment	1	6	0.45	0.529
genus	1	11	39.20	**<0.001**
status	1	11	4.67	0.054
genus × status	1	11	0.32	0.584
genus × treatment	1	95	0.32	0.575
status × treatment	1	95	0.00	0.986
genus × status × treatment	1	95	0.65	0.421
days	1	1072	675.56	**<0.001**
days × genus	1	1072	44.62	**<0.001**
days × status	1	1072	6.42	**0.011**
days × treatment	1	1072	3.83	0.051
days × genus × status	1	1072	9.11	**0.003**
days × genus × treatment	1	1072	6.98	**0.008**
days × status × treatment	1	1072	0.09	0.764
days × genus × status × treatment	1	1072	0.01	0.921
treatment × plot			-	-
genus × status × population			2.18	**0.015**
genus × status × treatment × unit			4.42	**<0.001**

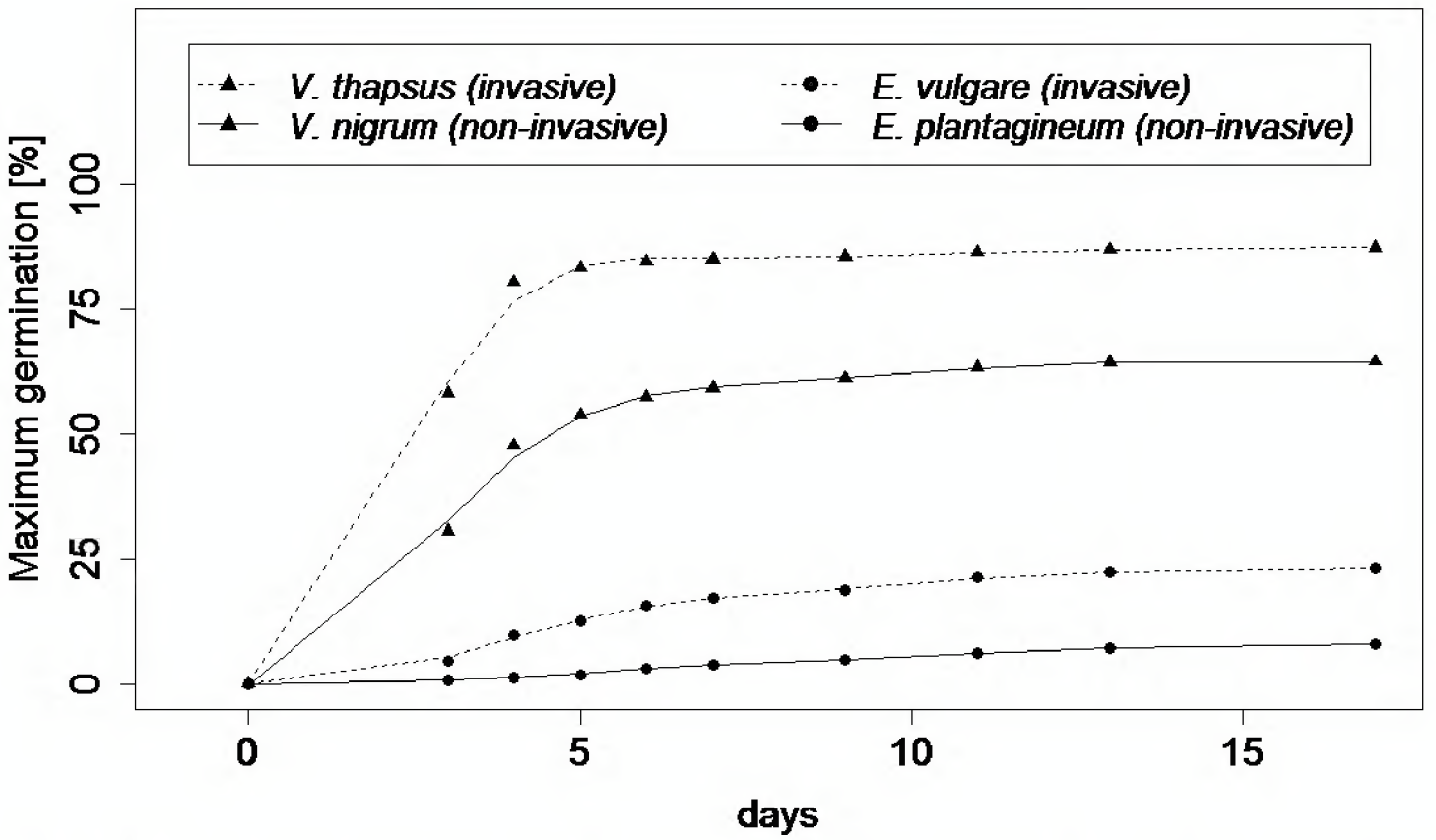

Figure 2. Germination development in the among-species approach testing for pre-adaptation of exotic (dashed line) and native species (solid line) of the genera *Echium* (circle) and *Verbascum* (triangle).

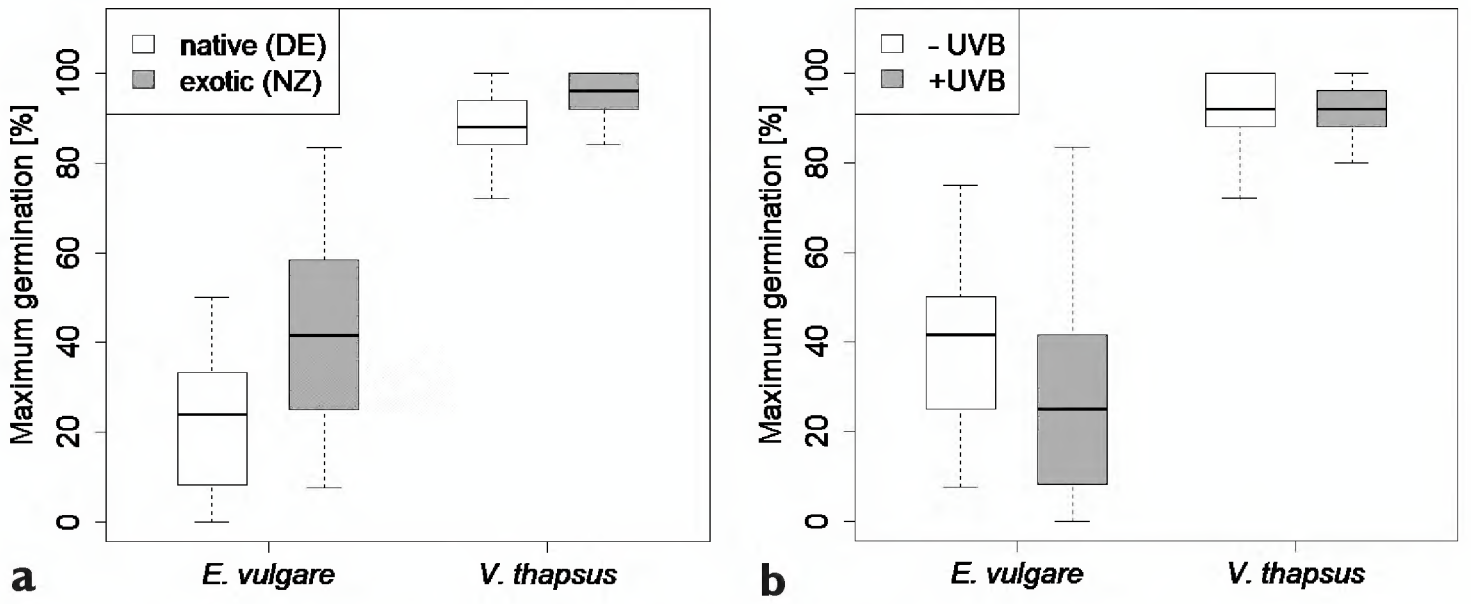

Figure 3. Maximum germination in the within-species approach testing for local adaptation of *Echium vulgare* and *Verbascum thapsus* seeds. **a** of New Zealand (grey) and German (white) populations and **b** in response to UV-B radiation (grey) and no UV-B radiation (white) treatment.

The within-species approach: Native vs. exotic origins

V. thapsus had a higher maximum germination success than *E. vulgare* (p=<0.001, Fig. 3). For both species, a significantly higher maximum germination was observed for exotic populations from New Zealand as compared to native German origins (p=0.004, Fig. 3a). The interaction between 'species' and 'origin' marginally failed to be significant but indicated a larger difference between native and exotic populations for *E. vulgare* than for *V. thapsus* by trend (p=0.051, Fig. 3a). Overall, the UV-B treatment did not lead to a significantly reduced germination success (p=0.055, Fig. 3b). However, a significant 'species × treatment' interaction showed a stronger effect of UV-B radiation on germination success of *E. vulgare* than of *V. thapsus* (p=0.003, Fig. 3b). A difference between native and exotic populations in response to high UV-B levels, as would have been displayed by a significant 'origin × treatment' interaction, was not found (Table 3).

The repeated measures analysis confirmed these results over time and revealed a faster germination of *Verbascum* seeds compared to *Echium* seeds and also a higher germination velocity of exotic origins of both species than native ones (Table 4). A significant threefold interaction effect of 'days', 'species' and 'origin' indicated a larger difference between native and exotic populations for *E. vulgare* than for *V. thapsus* (p=0.043, Table 4).

Discussion

The role of pre-adaptation

The among-species approach showed a higher maximum germination rate of invasive species compared to non-invasive congeners and an overall inhibiting effect of UV-B

Table 3. Results of the mixed model analysis of the within-species approach testing for local adaptation. Degrees of freedom (df_N = numerator, df_D = denominator), F-statistics (*F*) and significance values (*p*) are given. 'Treatment × plot' and 'species × origin × population' interactions were considered random effects and a Z-value instead of F-value is provided. Bold numbers indicate significant p-values ($p < 0.05$).

Source	df_N	df_D	*F/Z*	*p*
treatment	1	6	5.64	0.055
species	1	13	135.30	**<0.001**
origin	1	13	12.25	**0.004**
species × origin	1	13	4.63	0.051
species × treatment	1	109	8.97	**0.003**
origin × treatment	1	109	1.21	0.275
species × origin × treatment	1	109	2.26	0.136
treatment × plot			-	-
species × origin × population			1.81	**0.035**

Table 4. Results of the repeated measures analysis of the within-species approach testing for local adaptation. Degrees of freedom (df_N = numerator. df_D = denominator). F-statistics (*F*) and significance values (*p*) are given. 'Treatment × plot'. 'species × origin × population' and 'species × origin × treatment × unit' interactions were considered random effects and a Z-value instead of F-value is provided. Bold numbers indicate significant p-values ($p < 0.05$).

Source	df_N	df_D	*F/Z*	*p*
treatment	1	6	0.23	0.646
species	1	13	85.51	**<0.001**
origin	1	13	1.22	0.289
species × origin	1	13	0.18	0.680
species × treatment	1	109	0.14	0.706
origin × treatment	1	109	0.02	0.890
species × origin × treatment	1	109	0.38	0.542
days	1	1216	899.12	**<0.001**
days × species	1	1216	2.14	0.144
days × origin	1	1216	7.72	**0.006**
days × treatment	1	1216	1.00	0.317
days × species × origin	1	1216	4.12	**0.043**
days × species × treatment	1	1216	4.84	**0.028**
days × origin × treatment	1	1216	0.33	0.563
days × species × origin × treatment	1	1216	0.17	0.678
treatment × plot			-	-
species × origin × population			2.13	**0.017**
species × origin × treatment × unit			4.70	**<0.001**

radiation on germination success independent of the species' status. This positive association of rapid germination and high germination percentage of seeds of native origins with species' invasiveness has been also described in preceding studies (Radford and Cousens 2000, Cervera and Parra-Tabla 2009, Schlaepfer et al. 2010). In addi-

tion, a multi-species approach by Kempel et al. (2013), comparing 48 invasive and 45 non-invasive species, revealed the relevance of early life stages characteristics. In their study, in particular, propagule pressure and seed mass appeared to be important for the differentiation among species in order to predict species invasion success. Thus, these reproductive traits are likely to be beneficial characteristics, which directly increase establishment success of invasive species in the invaded range. A faster germination and higher germination rate have been described for invasive species, both in the native and invaded range, compared to the respective non-invasive species (Pyšek and Richardson 2007). Thus, these germination characteristics can be considered a pre-adaptation fostering invasiveness but will also become important traits under selection after the introduction of the species in a new range (Schlaepfer et al. 2010). However, the present study does not give an indication for a pre-adaptation of invasive species to high UV-B intensities, since different germination patterns between the two statuses in response to the UV-B treatment were not detected. This lack of evidence could be a consequence of the low number of congeneric species pairs included in the present study. A multi-species approach can be much more suitable to reveal existing pre-adaptation patterns (van Kleunen et al. 2010). Nevertheless, our findings display an overall negative effect of the abiotic factor UV-B radiation. The inhibiting effect of UV-B radiation on germination observed, both in the among-species and in the within-species approach of this study, has been previously described for several other species. Tevini et al. (1983), for example, confirmed reduced germination under high UV-B levels for three crop species. A similar result was found for *Bromus tectorum* (Dai and Upadhyaya 2002) and *Senecio jacobaea* (Tosserams et al. 1997). Thus, from a physiological perspective, UV-B radiation may indeed act as a selective agent for early life-cycle phases of plants species, even though its differential potential was not able to be shown.

The present study also indicates a stronger inhibition of germination under UV-B for *Echium* species, whereas *Verbascum* seeds, especially of invasive *Verbascum thapsus*, seem to be more UV-B tolerant. The tissues surrounding an embryo might act as UV-B shield, which could be a possible explanation of seed UV-B tolerance (van de Geijn et al. 1993). Various studies characterized the germination of *Verbascum thapsus* as strongly dependent on water, temperature and light (Gross 1980, Baskin and Baskin 1981, Gross and Werner 1982), whereas successful germination of this species is clearly reduced by shading (Semenza et al. 1978, Gross 1980). Possibly, due to the strong light affinity, highly developed photoprotection mechanisms can be assumed for *Verbascum thapsus*.

Evidence of recent adaptation

The within-species approach addressed the role of local adaptation in the invaded range and revealed a higher germination success of exotic origins of the invasive species from New Zealand compared to the native German populations. Again, stronger differences in germination proportions between exotic and native provenances were encountered

for the *Echium* species compared to *Verbascum*, in particular when considering progression with time. Beckmann et al. (2011) confirmed this result for three different exotic grassland species in New Zealand and suggested that local adaptation of germination patterns towards different temperature conditions in the exotic populations might be at play. Our data do not support the idea of a similar adaptation to the environmental factor UV-B radiation, since the maximum germination of both origins was reduced to the same extent by the UV-B treatment. Admittedly, as the seeds used in this study are field-collected or obtained from seed companies, it is hard to disentangle, whether altered germination patterns across ranges are truly adaptive or superimposed by maternal effects (Galloway 2001). Non-genetic effects, i.e. differences in handling or maternal effects have proven to hamper the interpretation of adaptive processes (Kawecki and Ebert 2004). This caveat can be overcome by referring to seed material from F1 offspring of sampled populations in future experiments. Furthermore, the included populations do not represent the broad distribution range of the study species and populations originating from other parts of the native range than sampled may display a different response, thus, making general deductions more difficult. However, differences between invasive and native populations might suggest a genetic shift due to evolutionary processes in the invaded range. Nonetheless, the encountered effects cannot directly be attributed to UV-B radiation, and might also be a consequence of other environmental factors in the habitat, which affect plant individuals in a similar way and cause comparable plant responses: The underlying selection pressure towards higher and faster germination might be caused, e.g., by water supply. In particular drought, which can evoke similar plant responses as UV-B (Tevini et al. 1981, Hofmann et al. 2003), is a factor to be considered, preferably in interaction with UV-B. UV-B effects interact with irradiation intensity and with exposure to drought (Hofmann and Campbell 2011), affecting physiological responses in grassland habitats, and thus the interaction of such factors for germination attributes need to be more critically taken into consideration in future studies.

Conclusions

The present study confirmed a distinctly inhibiting effect of UV-B radiation on germination of the studied species, but did not provide evidence for a UV-B specific pre-adaptation of invasive species or local adaption of exotic populations to UV-B in the invaded range. The overall reducing effect of UV-B radiation on germination suggests that UV-B represents an important selection factor in the invaded range, and particularly for alien species colonizing new habitats in parts of the southern hemisphere. Possibly, neither pre-adaptation nor local adaptation fully explains the invasive potential of the study species. Instead, the phenotypic plasticity to a broad range of environmental conditions in terms of a 'general-purpose genotype', as was already mentioned for *Verbascum thapsus* (Parker et al. 2003), might be of higher relevance (but see: van Kleunen et al. 2011).

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Supplementary material 1

Seed origins and population locations

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Data type: occurence data

Explanation note: Overview on seed origins of the study species and locations of the populations used in the experiment. Numbers in brackets indicate the number of populations within the respective group. DE = Germany, NZ = New Zealand, ES = Spain, NL = The Netherlands.

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